Movement activity and space use

– how does the moose react when the tourists come?

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Abstract

Fear of predation is a major selective pressure for prey species and, although important for survival, can have adverse effects on the well-being of the animals. Human disturbance has been shown to elicit the same behavioural and physiological responses, in particular in hunted species. Using GPS-data from a heavily hunted moose population in northern Sweden, I investigated differences in habitat selection and activity patterns between two valleys contrasting in human disturbance, during both peak and low tourism seasons. The effects of temperature, precipitation, and wind speed were also considered. I found moose to alter their habitat utilisation to use more protective habitats during the peak tourism seasons in the valley with high human disturbance, whereas open habitats were used more in the valley with low disturbance. I found no evidence for activity patterns being impacted by tourism, and the weather variables were of low importance. My study suggests that moose habitat selection is indeed affected by increased human disturbance. There is a need for studies on the long-term impacts on fitness on this displacement of moose into protective habitats. In addition, bodily measurements are required to assess physiological stress responses that are not visible in the behaviour of the animals. These findings, in combination with future studies, can help managers with the planning of further recreational sprawl into moose habitats.

Keywords: Moose, *Alces alces*, home range, habitat selection, tourism, human disturbance, activity, acceleration, movement, speed, seasons, sunlight phases, weather

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1. Introduction

As the human population is growing, we are continuously sprawling into previously undisturbed areas of nature. Development of infrastructure (e.g. Dulac, 2013), mineral exploitation (e.g. Edwards et al., 2014), and dam construction (e.g. Finer and Jenkins, 2012), are all having severe impacts on environmentally important ecosystems. Even protected areas are being impacted; the adjacent buffer zones become occupied by human activity, rendering the protected areas susceptible to the edge effect (Barber et al., 2014), and lower quality habitats in between the protected areas reduce connectivity (Crooks et al., 2011).

In the post-industrialised part of the world, the forces of urbanisation have more or less levelled off. This is partly due to the majority of the land already being used; for example, new developments frequently make use of abandoned agricultural fields, resulting in less need for deforestation (Pili et al., 2017). Furthermore, establishment of protected areas reduces the risk of untouched or ecologically important areas being developed (Mose, 2007). However, the obvious and large-scale landscape changes of urbanisation and development are not the only ways humans affect ecosystems.

Even seemingly harmless recreational activities, like nature-viewing or hiking, will inevitably affect ecological components and disturb wildlife, regardless of how careful the visitor may be (Steven et al., 2011). Simply walking in a natural area damages vegetation and compacts the soil (Cole, 2004) and the presence of humans can alter the physiology and behaviour of wildlife (e.g. Steven et al., 2011). The public interest in nature-based recreational activities has been increasing since the turn of the century (Hall et al., 2008). This is regarded as a positive development from a conservation perspective, as ecologically important areas can be enjoyed without requiring human modifications. Nevertheless, it does prompt consideration of how recreational activities and human presence adversely impact wildlife.

Human disturbance has been shown to induce the same fearful behaviours in prey species, including ungulates, as predator presence does (e.g. Andersen et al., 1996; Stankowich, 2008; Ciuti et al., 2012). Thus, recreational activity, for example, can drive and shape the whole ecosystem just as the presence of a top predator would. Fear of predation is an important evolutionary element for any prey species (Brown

et al., 1999). This does not only apply when an attack is imminent, but also when anticipating the potential risk of a predator being near (Brown et al., 1999). Behavioural responses to this are either to increase vigilance (Laundré et al., 2001), which in turn decreases foraging efficiency, or to change the time allocated to different foraging areas (Wolff and Horn, 2003). 'Landscape of fear' (Altendorf et al., 2001; Laundré et al., 2001) is now a widely accepted term used to describe how prey species alter their behaviour and use of the landscape in order to avoid predation.

The moose population (*Alces alces*) in Fennoscandia is heavily hunted. In fact, even in areas where wolves are present, hunting is the main cause of mortality for moose (Sand et al., 2012). Ungulates in hunted populations are more sensitive towards disturbance from humans and flee at a greater distance (Stankowich, 2008). However, as Stankowich (2008) notes, the animals are likely to be alerted to and stressed by the disturbance before they reach the fleeing point. The population in question is also exposed to a range of human disturbances other than hunting, such as terrestrial and aerial motorised activities (e.g. snowmobiles and helicopters), hiking, and nature-watching. Several studies have found that while ungulates avoid the motorised vehicles (e.g. Seip et al., 2007), they have a stronger reaction to skiers and hikers (Stankowich, 2008; Neumann et al., 2010, 2011). This is likely due to learning the appearance of the predator, as suggested by Andersen et al. (1996). This is supported by other studies, such as Valkenburg and Davis (1985) who found that a caribou population that was commonly hunted from snowmobiles showed greater fear response to those than did other populations.

One of the behavioural responses in moose to perceived predation risk is a change in habitat selection (e.g. Wasser et al., 2011). Habitat selection is a trade-off between perceived costs and benefits that will vary naturally with individual and environmental circumstances (Dussault et al., 2005). For example, cows with calves are more likely to seek protective cover, whereas males are more likely to choose high-quality foraging patches over shelter (Main, 2008). Similarly, optimal foraging choices can vary between populations depending on available habitats and vegetation. In the alpine areas, for example, the deciduous forest areas should offer higher forage availability for moose as a browser compared to the open tundra vegetation (Tape et al., 2016). The cost-benefit relationship of habitat selection can also change on a circadian basis; daylight increases both visibility to predators and risk of heat stress, whereas darkness offers protection from both, even in an open landscape (Nikula et al., 2004).

Similar to other ungulate species, moose show a crepuscular activity pattern (Cederlund, 1989; Cederlund et al., 1989), but this can be altered by external factors. Perceived predation risk can result in a population adjusting their daily

activity to avoid the predator (Ensing et al., 2014; Higdon et al., 2019). Ambient temperature is another influential factor, especially in large-bodied endotherms, such as the moose (Mitchell et al., 2018; Montgomery et al., 2019). Several studies have found ambient temperatures to impact moose movement and activity patterns, showing that moose are less active with increasing temperatures (Ericsson et al., 2015) and alter their daily activity pattern to be more active at night during warm periods (e.g. Street et al., 2015; Montgomery et al., 2019). Higher temperatures also alters habitat use in favour of thermal shelter, potentially resulting in the selection of habitats that are suboptimal for foraging in order to facilitate thermoregulation (Melin et al., 2014; Street et al., 2015).

Physiological responses to temperatures above the thermal threshold of moose include increased heart, respiratory, and metabolic rates (Græsli et al., 2020; Thompson et al., 2020). In captive moose, ambient temperatures above 14°C degrees in the summer and above 5°C in the winter have been found to induce heat stress (Renecker and Hudson, 1990; Dussault et al., 2004). This threshold has not been found in wild moose (Montgomery et al., 2019; Græsli et al., 2020), but, as suggested by Græsli et al. (2020), this could be a result of behavioural responses to mitigate the heat stress. Increasing temperatures are nevertheless suspected to have adverse effects on survival in moose populations in the southern bioclimatic edge (Murray et al., 2006; Lenarz et al., 2009).

1.1. Aims and purposes

Through this study, my aim is to find out if and how the moose behaviour is affected by disturbances from various tourism activities year around. Particularly, whether habitat selection, space use, and activity patterns are altered during peak tourism season. Furthermore, I aim to investigate how ambient temperature, precipitation, and wind speed affect those aspects of moose behaviour. Although the moose population in Fennoscandia is currently doing well, the warming climate risk making their status more vulnerable. It is therefore vital to know how tourism influences their behaviour, as this can otherwise be a cumulative factor that puts the population at risk. Thus, the findings of this study could aid natural resource management in making decisions favourable for moose survival, such as potentially directing certain types of activities to areas less important to the moose or ensuring a certain amount of canopy cover in areas where it is possible.

Using GPS-data from moose in two geographically adjacent valleys contrasting in human disturbance, I will investigate moose habitat selection, movement rate, and activity in relation to tourism pressure and weather.

Based on previous research, I hypothesise the following:

1. Moose habitat selection and space use will differ between the valleys with high and low tourism disturbance. I expect the moose will more frequently choose sub-optimal habitats in the valley with higher disturbance, and thus have a wider range of movement.
2. The moose in the valley with high tourism disturbance will display higher activity at night than those in the calmer valley, both in terms of estimated movement rates (distance moved per time unit) and acceleration data.
3. Within seasons, moose space use and activity pattern will change with changing tourism pressure. As the tourism pressure is low, moose behaviour is expected to be similar between the valleys as they will then have the same disturbance level.
4. Higher ambient temperature will change the activity patterns for the moose in both valleys in similar ways. Higher temperatures will lower the activity and movement rate.

2. Methods

2.1. Study area

The study area was placed near the alpine village of Nikkaluokta in Norrbotten, Sweden (67°51´N, 19°0´W, Figure 1). This is likely one of the most motorised areas in the Swedish mountain chain, and the moose here mainly utilise two valleys contrasting in human disturbance. The Ladtjo valley leads from Nikkaluokta to Kebnekaise, Sweden's highest mountain, and is subsequently subjected to heavy tourism. The Vistas valley, on the other hand, is exposed to much less human activity.

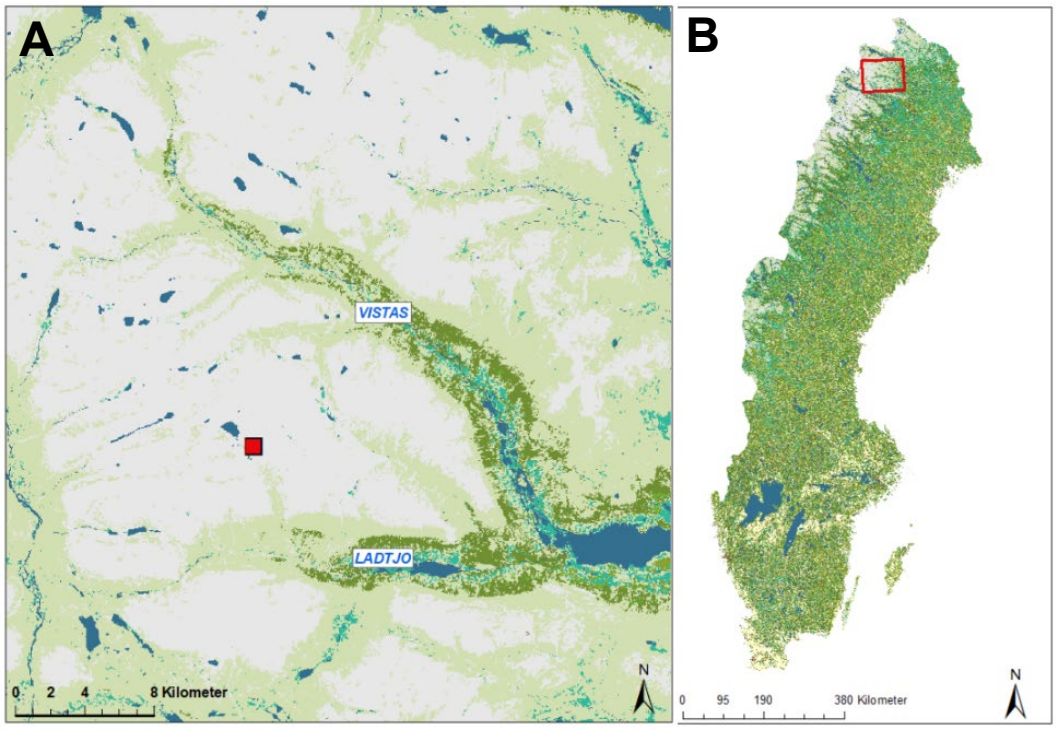

Figure 1. Maps showing the study area in Nikkaluokta. (A) shows the two valleys, Ladtjo and Vistas. The red square marks the location of the weather station Tarfala A. In (B), the box outlined in red shows where in Sweden the study area is.

2.2. Data collection

2.2.1. Moose activity and movement rates

Movement and activity data were collected over 12 years (2008-2019), tracking 37 individual adult moose (24 females, 13 males) from the population in Nikkaluokta, northern Sweden. Figure 2 shows how many moose were tracked for each year of the study period. During tagging, the moose were tranquilized and anaesthetized from a helicopter using a dart gun (ethical approvals: DNR A116-09, A12-12, A14-15, A3-16, A28-17). Each moose was then equipped with a GPS collar with temperature and activity sensor (VECTRONIC Aerospace, Germany). For the first year after marking an individual, the GPS collar sent the positions every 30 minutes. After the first year, the positions were instead calculated with 3-hour intervals. The activity sensors on the collars collected acceleration data, on an x- and a y-axis. The x-axis measured the anteroposterior movements (forwards /backwards) and the y-axis measured the dorsoventral movements (up/down). These were given as 5-minutes averages between 0 and 255. A value closer to 0 meant the animal was sedentary, whereas a higher value showed increased activity.

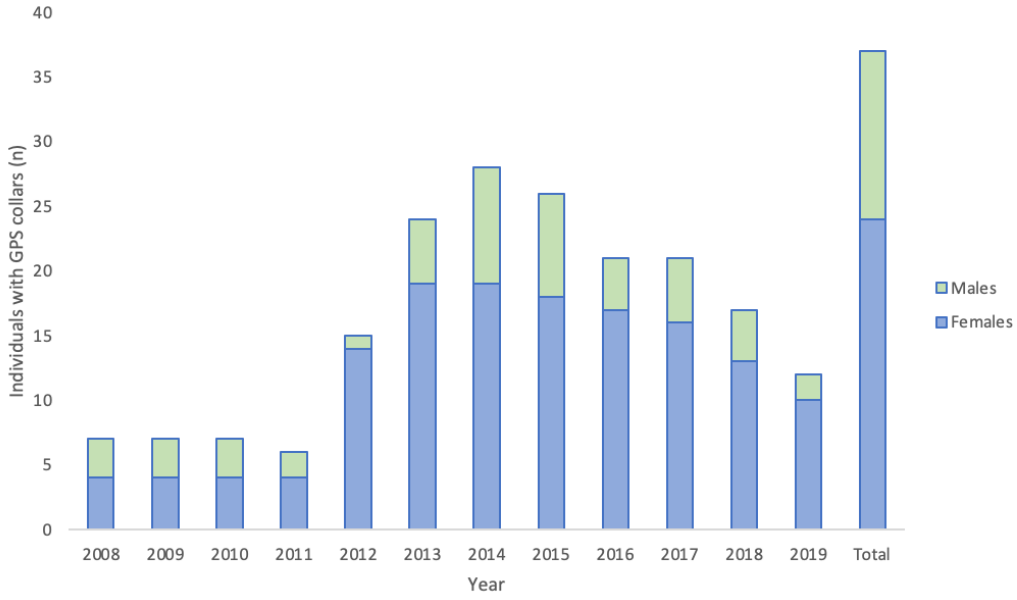

Figure 2. The number of individual moose tracked each year during the study period, also showing how many of each sex. The last column shows the total number that was analysed in this study.

2.2.2. Tourism data

I obtained the daily tourism data in the form of number of guests per night between 01 January 2008 and 31 August 2019 from Statistics Sweden (Statistics Sweden, 2019). In line with their privacy policy, I received a compilation of the statistics from 21 accommodation facilities in the vicinity of the study area (Appendix 1). In order to find out how guest intensity has changed over the years, I calculated the sum of guest nights per year. I then tested the correlation between the sum of guests and the year. However, here I excluded 2019 as I only had data until the 31 August that year.

2.2.3. Weather data

I downloaded the weather data (ambient temperature, precipitation amount and type, and windspeed) from the Swedish Meteorological and Hydrological Institute (SMHI, 2019b), from the active weather station Tarfala A in the study area (67.9124°N, 18.6101°E; see figure 1). All variables apart from windspeed were available in daily averages. The original data for windspeed was reported on an hourly basis, which I used to calculate the daily averages.

The air temperature was also recorded on the GPS-collars on the moose, giving an extra estimate on ambient temperature (Ericsson et al., 2015). This data was thus recorded at the same time intervals as the positions of the animal (see section 2.2).

2.2.4. Vegetation data

I downloaded the national ground cover data from the Swedish Environmental Protection Agency (Naturvårdsverket, 2019), from which I extracted and reclassified the vegetation types that were relevant for my study. I used the habitat classes ‘conifer forest’, ‘deciduous forest’, ‘mixed forest’, ‘open habitat’, ‘water’, and ‘other’ (details in Appendix 2). In the study area, most deciduous forest is mountain birch forest (predominantly *Betula pubescens czerepanovii*), and the open habitat is mainly composed of treeless tundra vegetation.

2.3. Subdividing the data

After plotting the positions of the moose, I identified and removed one outlier. I furthered filtered the data to only contain the data between minute 55 and 05, thus removing all the information sent from the GPS-collar on the half-hour mark while still ensuring all the full-hour data was kept. For my analyses, I used Julian day based on dates of a given position.

Using *segmented* package (Muggeo, 2017) in RStudio (version 1.2.5019; R Core Team, 2018) to identify breakpoints in the amount of guest nights, I subdivided all data into 4 separate periods with different tourism pressure under different climatic seasons (Figure 3, table 1). To ensure the climatic seasons were correctly identified for the study area, I used the season arrival maps at SMHI (SMHI, 2019b). This function contained data from 2015 and did thus not cover my full study period; nevertheless, it gave approximate information about the seasons in the study area. As the subdividing was determined by guest nights and not season, this was deemed to be sufficient for its purpose.

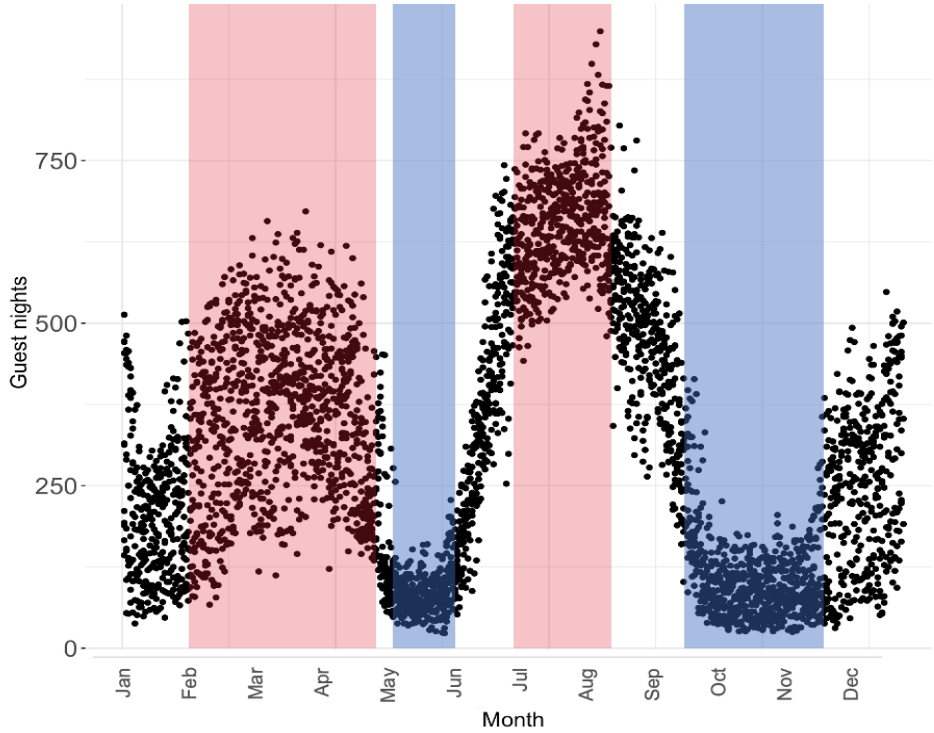

Figure 3. Number of guest nights in the study area during the study period (2008-2019) for each Julian day of the year, with the timeline displayed as the months. The shaded areas are the subdivided periods used in my study; red for the tourism peaks and blue for the lows.

Table 1. The four subsets the data was divided into, as pictured in Figure 3 above, and the Julian day period and dates of the year they correspond to.

Period name	Day start	Day end
Winter Peak	30 (30 Jan)	118 (28 Apr)
Spring Low	124 (04 May)	162 (11 Jun)
Summer Peak	182 (1 Jul)	229 (17 Aug)
Autumn Low	263 (20 Sep)	328 (24 Nov)

2.4. Analysis

2.4.1. Utilisation distribution

Using their position data, I identified the moose individuals who used each valley. I then filtered the data to only include individuals who utilised either Vistas or Ladtjo valley, removing the ones who used both valleys (n=10). This left 27 moose for my analysis. I used the biased random bridge approach in order to estimate moose home range (utilised more than 95% of the time) based on utilisation distribution given by their relocations (R package *AdehabitatHR*; Calenge, 2005). Using tools available in the R package *raster* (Hijmans, 2019), I extracted the land cover data within a given moose home range. To test for difference in habitat utilisation between moose in relation to tourism activity, I correlated moose utilisation distribution to the habitat classes and valley using a generalised linear mixed model (R package *lme4*; Bates et al., 2015). To account for autocorrelation within the data, repeated measures, and differences among individual moose, I assigned moose ID as random factor.

2.4.2. Activity, movement rates, and weather

The acceleration data from each individual's GPS-collar contained an x and a y-value, indicating horizontal and vertical head movement. In line with the method of Berger and Dettki (2009), I calculated an average value from these two. As I required the acceleration data per hour to be comparable to other data, I further calculated an hourly mean. To calculate moose movement speed (m/h), I calculated the Euclidean distance between two following relocations and divided it by the time elapsed (R package *adehabitatHR*; Calenge, 2005).

I determined the position of the sun for each time stamp in my dataset (R package *suncalc*; Thieurmel et al., 2019). I summarised the definitions into four categories; dusk, dawn, day and night and matched it to the relocations of the moose (for details, see Appendix 3).

A time period in one of my subsets (*Spring Low*) coincided with the summer solstice, meaning I was unable to specify day and night using information on sunset and sunrise (i.e., the sun never left the horizon). For this period, I instead categorised day and night based on set time intervals with human activity in mind; from 08.00 to 20.00 was categorised as day, and 20.01 until 07.59 was classified as night.

To determine which factors that were most influential for movement rate and activity, respectively, I used model averaging based on Akaike Information Criterion (AICc, R package *MuMIn*; Barton, 2020). I also included daily guest nights in this calculation, as this value still varied between my subdivided periods. For my final model, I included the five most influential factors (Appendix 4). Sex was included in the model averaging but was not found to be of enough importance to be included in the final model.

To capture different aspects of moose response to human activity, I tested moose activity (i.e. acceleration) and movement rate (i.e. displacement) separately using a linear mixed model (R package *nlme*; Pinheiro et al., 2018), with the factors that were identified to be of importance. As the data was not normally distributed, both response variables were first transformed into their natural logarithm. To account for data from several years for a given moose, I assigned individual and year as random factors with year nested in moose individual. To avoid too many interaction terms (i.e. valley, daytime, and period) in the same model and to simplify it as much as possible, I decided to analyse the four subdivided periods separately, including only a single interaction term for a given period (i.e. valley and daytime). As a result, I could compare the model outputs from the four periods to each other. For each linear mixed model produced, I estimated the predicted values for the response (R package *ggeffects*; Lüdecke, 2018).

3. Results

Out of the 27 moose I used in the analysis, 12 had their home range in Ladtjo valley (7 females, 5 males), and 15 had theirs in Vistas valley (11 females, 4 males). The tourism in the area has increased gradually over the period of the study ($r=0.93$, $p<0.001$).

3.1. Habitat selection and space use in the two valleys

The percentage of available habitat types was similar in the two valleys, with open areas (i.e. tundra) and deciduous forest (i.e. mountain birch forest) being the dominant habitat (Figure 4).

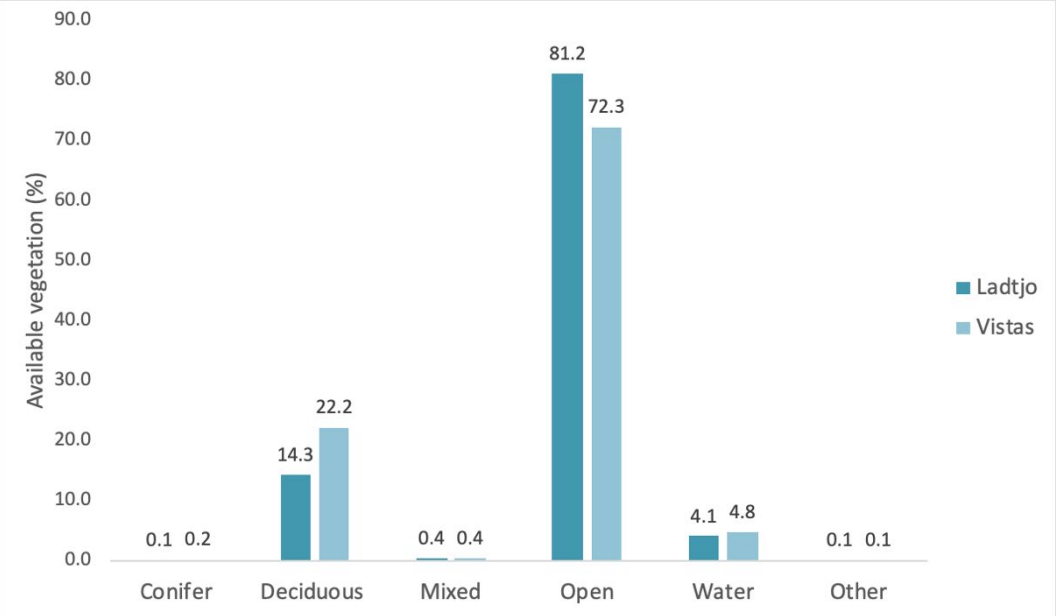

Figure 4. The habitat types available (%) in Ladtjo and Vistas valley. Open habitat was the dominating habitat in both valleys.

The home range size did not differ significantly between the valleys in *Winter Peak* period, but in all other periods the home range was larger in Ladtjo valley than in Vistas (*Winter Peak*: t(1,16) = -0.76, *p*=0.458, *Spring Low*: t(1,16)= -2.41, *p* = 0.003; *Summer Peak*: t(1,15)=-3.28, *p*=0.005; *Autumn Low*: t(1,15)=-2.24, *p* = 0.041; Figure 5). The average home range size for each valley and season are listed in Table 2.

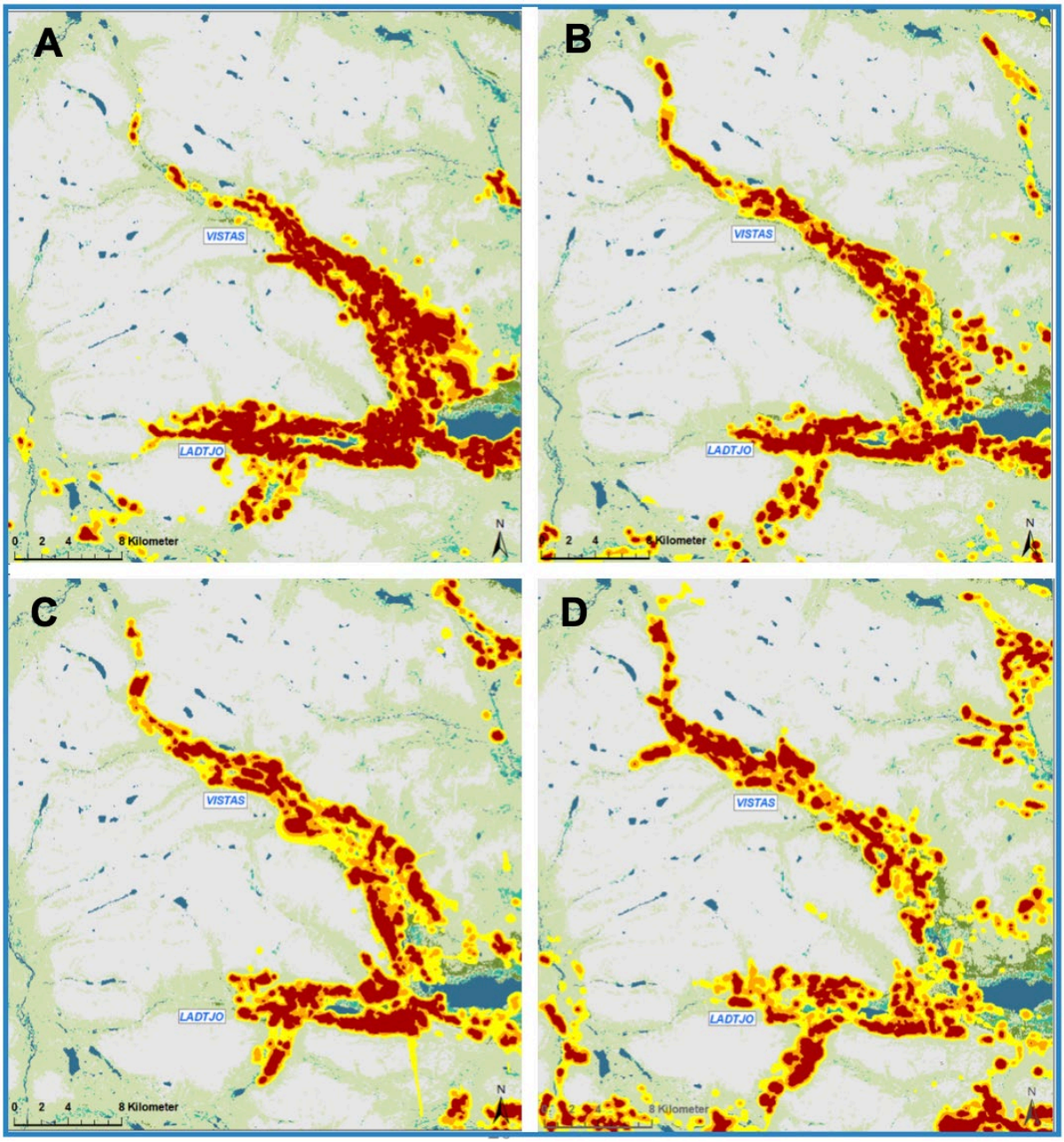

Figure 5. The home and core ranges of moose during (A) Winter Peak *season, (B)* Spring Low *season, (C)* Summer Peak *season, and (D)* Autumn Low *season. The home ranges (95% utilisation) are shown in yellow, the core (50% utilization) in red, and the intermediate (75% utilization) in orange.*

Table 2. The average home range sizes (km^2) and standard deviation for each season and valley.

	Winter Peak		**Spring Low**		**Summer Peak**		**Autumn Low**	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Ladtjo	8.70	5.03	15.98	11.72	23.08	18.46	20.04	10.07
Vistas	7.49	3.34	5.95	3.10	10.23	4.99	11.46	5.34

During all seasons, deciduous forest was an important habitat for moose in both valleys (Table 3). In both the peak tourism seasons, moose in Vistas valley (low human activity) used open habitats more than moose in Ladtjo valley, whereas there was no difference in habitat utilisation between the valleys during the low tourism seasons (Table 3).

In the *Winter Peak* tourism season, I found that moose favoured deciduous forest over open habitats and water (Table 3a). When looking at the interaction between valley and habitat types, moose used water and open habitats significantly more in Vistas valley than in Ladtjo valley, with the use of water habitat displaying the largest difference (Table 3a).

During *Spring Low* season, I found that moose were more in deciduous forest than in conifer forest, mixed forest, and open habitat (Table 3b) in both valleys.

Similar to in the *Spring Low* season, my results for *Summer Peak* season showed significantly lower utilisation of conifer and mixed forest compared to deciduous forest by moose in both valleys (Table 3c). As in *Winter Peak* season, the *Summer Peak* utilisation showed that moose favoured deciduous forest over water and open habitats (Table 3c). Comparing the habitat utilisation between the valleys, I found that open habitats was used more in Vistas valley than in Ladtjo valley (Table 3c).

During *Autumn Low* season, my results indicated that moose used more open habitats than deciduous forest (Table 3d). There was also an indication that conifer forest was used less than deciduous forests in Vistas valley than in Ladtjo valley (Table 3d).

Table 3. Estimates and standard errors of moose utilisation in relation to habitat as given by the generalised linear mixed model, 2008-2019. Deciduous forest as intercept and moose assigned as random factor. Ladtjo valley is intercept for valley comparisons.

A. Winter Peak					**B. Spring Low**			
	Estimate	SE	z-value	Pr(>|z|)	Estimate	SE	z-value	Pr(>|z|)
Intercept	-0.75	0.04	-18.3	<0.001**	-0.94	0.05	-20.0	<0.001**
Conifer	-0.04	0.10	-0.4	0.680	-0.22	0.07	-3.1	0.002*
Mixed	-0.04	0.11	-0.4	0.709	-0.16	0.10	-1.7	0.093
Open	-0.16	0.02	-0.8	<0.001**	-0.04	0.02	-2.1	0.037
Water	-0.47	0.05	-8.7	<0.001**	0.01	0.04	0.3	0.759
Other	-0.20	0.36	-0.6	0.580	-0.12	0.48	-0.3	0.795
Vistas	-0.04	0.05	-0.7	0.473	0.08	0.06	1.3	0.207
Conifer:Vistas	-0.19	0.18	-1.1	0.274	0.05	0.16	0.4	0.728
Mixed:Vistas	0.01	0.19	0.1	0.962	-0.04	0.20	-0.2	0.840
Open:Vistas	0.10	0.03	3.2	0.002*	-0.04	0.03	-1.2	0.219
Water:Vistas	0.27	0.09	2.9	0.004*	-0.07	0.06	-1.2	0.215
Other:Vistas	-0.58	2.66	-0.2	0.828	0.53	0.76	0.7	0.485
C. Summer Peak					**D. Autumn Low**			
	Estimate	SE	z-value	Pr(>|z|)	Estimate	SE	z-value	Pr(>|z|)
Intercept	-0.84	0.06	-14.3	<0.001	-1.14	0.06	-18.4	<0.001
Conifer	-0.43	0.04	-9.5	<0.001**	0.17	0.12	1.5	0.140
Mixed	-0.22	0.07	-3.0	0.003*	0.13	0.12	1.1	0.295
Open	-0.20	0.02	-10.4	<0.001**	0.14	0.03	5.5	<0.001**
Water	-0.48	0.05	-9.9	<0.001**	-0.01	0.04	-0.3	0.764
Other	-0.40	0.61	-0.7	0.510	0.08	0.29	0.3	0.763
Vistas	-0.09	0.08	-1.1	0.288	0.07	0.08	0.9	0.393
Conifer:Vistas	0.06	0.11	0.5	0.594	-0.47	0.25	-1.9	0.063
Mixed:Vistas	-0.02	0.14	-0.1	0.888	-0.32	0.21	-1.5	0.125
Open:Vistas	0.17	0.03	6.2	<0.001**	-0.04	0.04	-1.2	0.233
Water:Vistas	0.12	0.07	1.7	0.096	-0.07	0.06	-1.1	0.290
Other:Vistas	0.05	0.80	0.1	0.949	-0.45	1.08	-0.4	0.679

3.2. Diurnal and seasonal differences in activity and speed

3.2.1. Diurnal and seasonal differences in activity

In all periods, moose were differently active between day and night (as indicated by differences between acceleration levels), although for *Winter Peak* and *Spring Low* the estimated values were low (Table 4). Activity did not differ significantly between the valleys overall, but moose showed different activity patterns between the valleys in the winter peak and autumn low tourism seasons. For all periods, guest nights were significant although with low estimate values, meaning the impact on activity was negligible in relation to the other covariates tested (Table 4).

In *Winter Peak* season, I found that moose were significantly more active during dawn and dusk compared to during the day in both valleys (Table 4a). Comparing the valleys, moose were more active at dawn and dusk in Vistas than in Ladtjo valley, although the estimated values indicated only a small difference (Figure 6a, Table 4a).

During *Spring Low* season, the activity at night was lower than at daytime (Table 4b). As the statistical model for this season only included day and night, I did not get any results for dusk and dawn (Figure 6b, Table 4b).

Summer Peak season showed dusk as the most active sunlight phase (Figure 6c, Table 4c), but there was no difference between the valleys.

In *Autumn Low* season, both dawn and dusk showed an increase in activity for both valleys. Comparing the valleys, the moose were more active at dawn and dusk in Vistas valley than in Ladtjo during this season, although the estimated values were low (Figure 6d, Table 4d).

Table 4. The estimates and standard errors, t-value, and p-value given by as given by the linear mixed model for moose acceleration levels at different times of the day. Day and Ladtjo valley were used as reference in the intercept and moose individual was as random factor.

A. Winter Peak					**B. Spring Low**			
	Estimate	SE	t	p	Estimate	SE	t	p
Intercept	1.03	0.07	15.8	<0.001**	1.71	0.11	15.7	<0.001**
Dawn	0.37	0.02	23.7	<0.001**	-	-	-	-
Dusk	0.31	0.02	19.9	<0.001**	-	-	-	-
Night	-0.06	0.01	-6.4	<0.001**	-0.18	0.01	-13.6	<0.001**
Vistas	-0.07	0.09	-0.8	0.438	-0.05	0.15	-0.3	0.763
Guest nights	0.0001	0.00	3.7	<0.001**	-0.0007	0.00	-8.3	<0.001**
Dawn:Vistas	0.04	0.02	2.0	0.049*	-	-	-	-
Dusk:Vistas	0.08	0.02	3.9	<0.001**	-	-	-	-
Night:Vistas	0.02	0.01	1.9	0.064	-0.00	0.02	0.4	0.864
C. Summer Peak					**D. Autumn Low**			
	Estimate	SE	t	p	Estimate	SE	t	p
Intercept	2.51	0.13	19.2	<0.001**	1.31	0.11	11.5	<0.001**
Dawn	0.14	0.16	0.8	0.406	0.54	0.02	33.4	<0.001**
Dusk	0.40	0.15	2.6	0.009*	0.33	0.02	20.7	<0.001**
Night	0.14	0.01	10.3	<0.001**	0.05	0.01	4.4	<0.001**
Vistas	0.07	0.17	0.4	0.674	-0.004	0.16	-0.03	0.978
Guest nights	-0.0007	0.00	-14.0	<0.001**	0.0004	0.00	7.1	<0.001**
Dawn:Vistas	-0.08	0.00	-0.4	0.702	0.07	0.02	3.4	<0.001**
Dusk:Vistas	-0.17	0.21	-0.8	0.500	0.06	0.23	2.7	0.007*
Night:Vistas	-0.01	0.02	-0.9	0.387	0.03	0.02	1.6	0.150

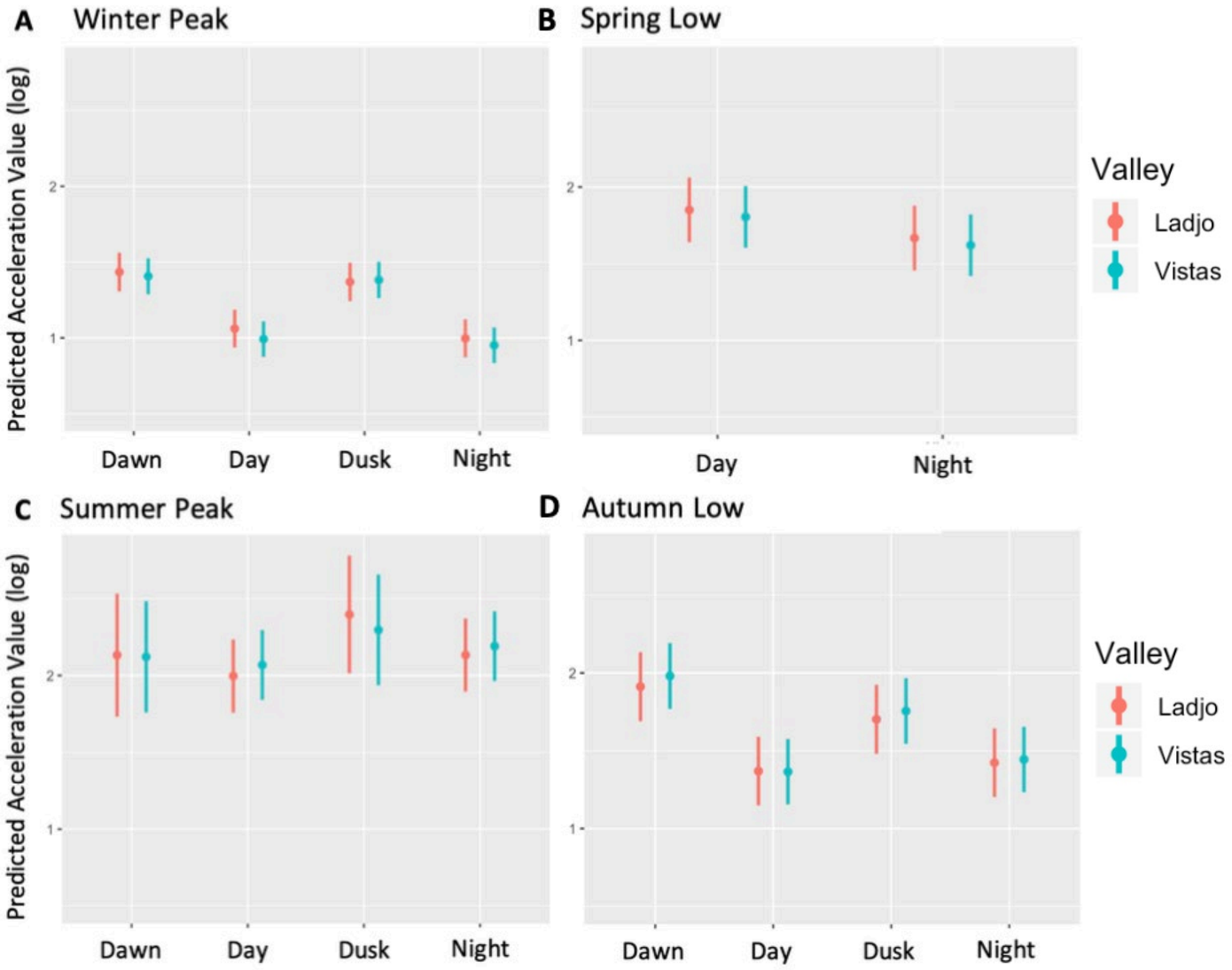

Figure 6. The predicted acceleration levels (log-transformed) and the standard errors for the time of day during (A) Winter Peak *period, (B)* Spring Low *period, (C)* Summer Peak *period, and (D)* Autumn Low *period.*

3.2.2. Diurnal and seasonal differences in movement rates

In all four subdivided seasons, moose differed in their movement rates (m/h) between day and night. In *Winter Peak*, *Spring Low*, and *Autumn Low*, all moose moved at a slower speed during night compared to daytime, whereas during the *Summer Peak* season, moose switched their movement patterns to moving more during the night instead (Figure 6, Table 5). No overall differences between the valleys were found, but timing of moose movement differed between the valleys at dawn in *Winter Peak* season, and at dusk in *Autumn Low* season. Guest nights were significant for *Winter Peak* and *Summer Peak* although with negligible estimate values, meaning the impact was low (Table 5).

During *Winter Peak* season, I found a significant increase in moose movement rate (m/h) during dawn and dusk, with a decrease in speed during the night (Table 5a). My results also indicated that the moose moved less at dawn and dusk in Vistas valley than in Ladtjo valley, although the estimates were low (Figure 7a, Table 5a).

In *Spring Low*, I did not find any other differences in movement rate than between night and day (as mentioned above). However, as with the analysis for the acceleration, *Spring Low* contained neither dawn nor dusk (Figure 7b, Table 5b).

My results for *Summer Peak* season showed significantly higher movement rate during dawn and dusk than during the day in both valleys (Figure 7c, Table 5c).

During *Autumn Low* season, the moose moved at higher rates at dawn than daytime. Between the valleys, the rate of movement was higher at dusk in Vistas valley than in Ladtjo (Figure 7d, Table 5d)

Table 5. The estimates and standard errors, t-value, and p-value given by the linear mixed model for moose movement rate (m/h) at different times of the day. Day time and Ladtjo valley were used as reference in the intercept and moose individual as random factor.

A. Winter Peak					**B. Spring Low**			
	Estimate	SE	t	p	Estimate	SE	t	p
Intercept	2.63	0.06	43.7	<0.001**	3.12	0.06	51.4	<0.001**
Dawn	0.18	0.02	9.6	<0.001**	-	-	-	-
Dusk	0.16	0.02	8.6	<0.001**	-	-	-	-
Night	-0.26	0.01	-21.7	<0.001**	-0.22	0.02	-13.2	<0.001**
Vistas	0.01	0.08	0.2	0.866	0.05	0.08	0.6	0.547
Guest nights	-0.0001	0.00	3.8	<0.001**	-0.0001	0.00	-1.3	0.200
Dawn:Vistas	-0.07	0.03	-2.6	0.009*	-	-	-	-
Dusk:Vistas	-0.05	0.03	-2.0	0.048	-	-	-	-
Night:Vistas	0.00	0.02	0.2	0.864	0.01	0.02	0.4	0.705
C. Summer Peak					**D. Autumn Low**			
	Estimate	SE	t	p	Estimate	SE	t	P
Intercept	3.73	0.09	39.6	<0.001**	3.32	0.07	44.3	<0.001**
Dawn	0.38	0.22	1.7	0.080	0.20	0.02	8.6	<0.001**
Dusk	0.90	0.21	4.4	<0.001**	-0.00	0.02	-0.1	0.889
Night	0.06	0.02	3.4	<0.001**	-0.32	0.02	-18.1	<0.001**
Vistas	0.05	0.10	0.6	0.586	0.02	0.10	0.2	0.848
Guest nights	0.0003	0.00	3.7	<0.001**	-0.0001	0.00	-1.1	0.253
Dawn:Vistas	-0.21	0.29	-0.7	0.465	0.05	0.03	-1.9	0.054
Dusk:Vistas	-0.14	0.28	-0.5	0.630	0.13	0.03	4.4	<0.001**
Night:Vistas	-0.02	0.02	-1.1	0.279	0.03	0.02	1.4	0.150

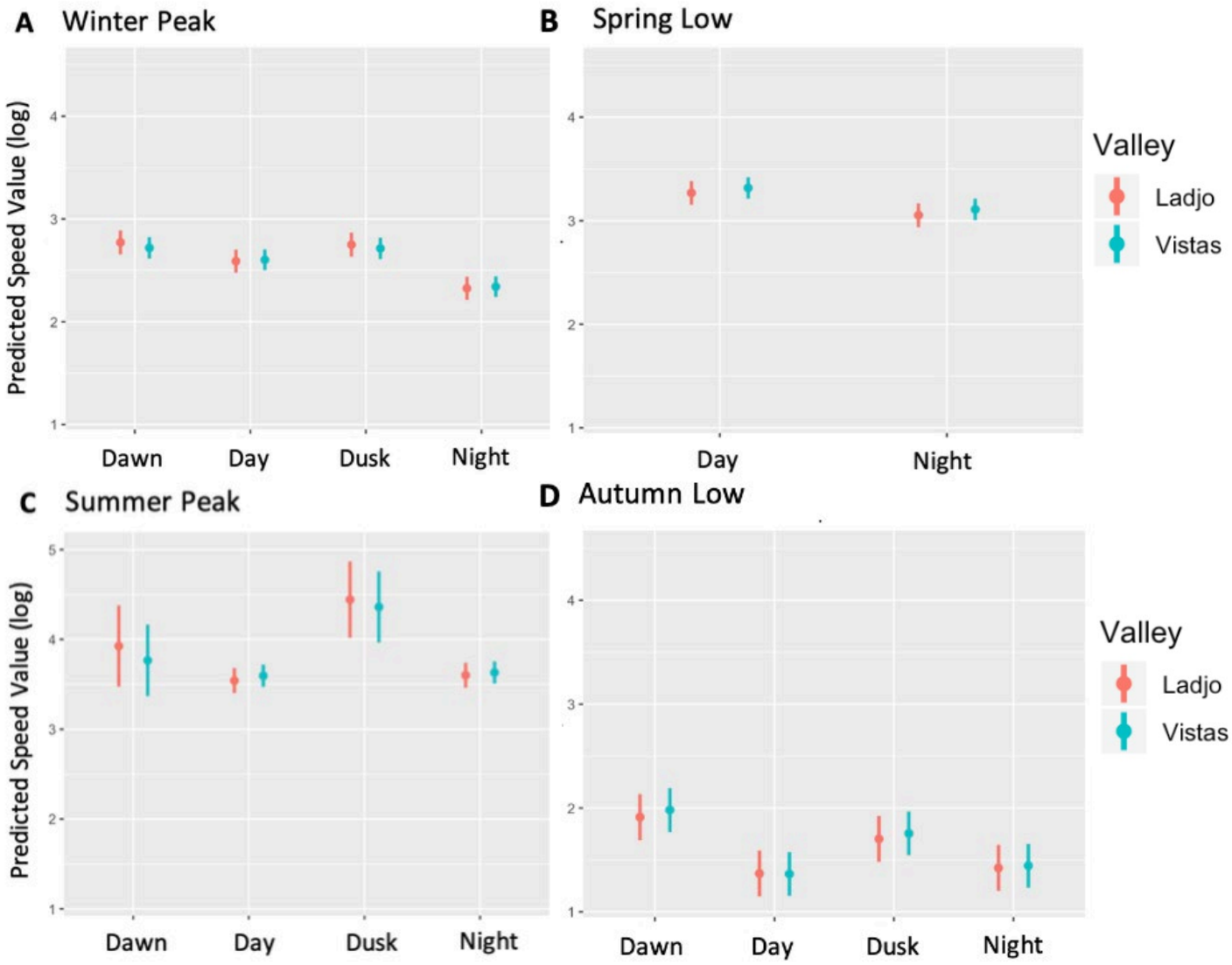

Figure 7. The predicted movement rates (log-transformed) and the standard errors for the time of day during (A) Winter Peak *period, (B)* Spring Low *period, (C)* Summer Peak *period, and (D)* Autumn Low *period.*

3.3. Impact of environmental factors

3.3.1. Impact of weather on activity

I found all weather variables to be of statistical importance in relation to moose activity (i.e. acceleration levels), although all estimates were 0.01 or lower in varying directions. This was the same for all subdivided periods (Table 6).

Table 6. The estimates and standard errors, t-value, and p-value given by the linear mixed model for weather factors impact on moose activity (acceleration data). Moose individual was used as random factor and Ladtjo as reference valley.

A. Winter Peak					**B. Spring Low**			
	Estimate	SE	t	p	Estimate	SE	t	p
Intercept	1.03	0.07	15.8	<0.001**	1.71	0.11	15.7	<0.001**
Wind speed	-0.01	0.00	-7.6	<0.001**	-0.01	0.00	-5.1	<0.001**
Precipitation	0.004	0.00	3.1	0.002*	0.003	0.00	2.6	0.010*
Temp station	-0.001	0.00	-2.1	0.033	0.06	0.00	46.3	<0.001**
Temp collar	0.01	0.00	15.0	<0.001**	-0.01	0.00	-12.2	<0.001**
C. Summer Peak					**D. Autumn Low**			
	Estimate	SE	t	p	Estimate	SE	t	p
Intercept	2.51	0.13	19.2	<0.001**	1.31	0.11	11.5	<0.001**
Wind speed	0.01	0.00	2.1	0.037*	0.005	0.00	2.82	0.005*
Precipitation	0.003	0.00	4.1	<0.001**	-0.003	0.00	-3.18	0.015
Temp station	0.01	0.00	5.1	<0.001**	0.01	0.00	6.94	<0.001**
Temp collar	-0.01	0.00	-9.7	<0.001**	0.01	0.00	6.35	<0.001**

3.3.2. Impact of weather on moose movement

The impact of weather variables on moose movement speed (m/h) was small. For all periods, both temperature measures were highly significant, although for *Winter Peak*, *Spring Low*, and *Summer Peak*, the two measurements impacted moose speed in different directions (Table 7). For *Autumn Low,* moose increased their movement with temperature. However, for all periods the estimate values were low (Table 7).

I found precipitation to affect moose movement speed only in *Spring Low* and *Autumn Low*, whereas moose changed their movement speed in relation to wind speed only in *Winter Peak* and *Autumn Low* (Table 7). However, in line with the other weather factors (e.g. precipitation and both measures of ambient temperature), the estimate values indicated these were of lower importance (Table 7).

Table 7.The estimates and standard errors, t-value, and p-value given by the linear mixed model for weather factors impact on moose movement rate (m/h). Moose individual was used as random factor and Ladtjo as reference valley.

Winter Peak					**Spring Low**			
	Estimate	SE	t	P	Estimate	SE	t	p
Intercept	2.63	0.06	43.7	<0.001**	3.12	0.06	51.4	<0.001**
Wind speed	-0.005	0.002	-3.2	0.002*	0.0001	0.003	0.0	0.969
Precipitation	0.001	0.002	-0.4	0.668	0.004	0.002	2.7	0.006*
Temp station	-0.003	0.001	-4.8	<0.001**	0.04	0.002	27.5	<0.001**
Temp collar	0.007	0.001	10.4	<0.001**	-0.01	0.001	8.1	<0.001**
Summer Peak					**Autumn Low**			
	Estimate	SE	t	p	Estimate	SE	t	p
Intercept	3.73	0.09	39.6	<0.001**	3.32	0.07	44.3	<0.001**
Wind speed	0.002	0.005	0.3	0.747	-0.01	0.002	-2.35	0.019
Precipitation	-0.001	0.001	-1.2	0.224	0.004	0.001	3.32	<0.001**
Temp station	0.04	0.002	17.8	<0.001**	0.01	0.001	7.76	<0.001**
Temp collar	-0.04	0.001	-35.1	<0.001**	0.01	0.001	4.90	<0.001**

4. Discussion

The outcome of my study can be summarised into four key findings. First, moose changed their habitat utilisation between the low and peak tourism seasons in the valley exposed to higher human activity. During the two peak seasons (*Winter Peak* and *Summer Peak*), moose in the calmer Vistas valley used exposed (i.e. open) habitats more than the moose in the busier Ladtjo valley, whereas this difference was not found for the low tourism seasons. Second, the moose home range sizes were significantly larger in Ladtjo valley than in Vistas in all periods apart from in *Winter Peak* season. Third, although the diurnal pattern varied between the seasons, I found no evidence that moose changed their diurnal activity or movement speed in response to tourism activity. The final finding concerns the weather variables; wind speed, precipitation, and both measurements of temperature all affected activity and movements speed. They were however of lower importance than the sunlight phases.

4.1. Implications of my results

4.1.1. Human impact on moose space use and habitat selection

During *Winter Peak* and *Summer Peak*, moose used significantly less habitat without cover in the Ladtjo valley (high human disturbance) than they did in the Vistas valley (low human disturbance). Previous studies have found female moose with calves to have a stronger selection preference for habitat with protection from predators than solitary moose (Dussault et al., 2005; Bjørneraas et al., 2012). Even though I did not analyse moose movement in relation to the presence of offspring, my results support this as the majority of the moose used in my study are females; particularly as the difference in habitat selection was not found between the valleys during the low tourism seasons. There are however other factors that can cause moose to change their habitat preference. Dussault et al. (2005) found all moose to prefer habitats offering protection from the snow during winter. However, if this was the reason for moose preferring protective habitats in my study, there should

be similar patterns in the Vistas valley during *Winter Peak* season, which there is not. This therefore supports the hypothesis that the moose choices of foraging patches are impacted by the tourism levels.

Another aspect to consider is how the available forage affects the habitat selection. In summer, the diets of the Fennoscandian moose include a wide variety of plant species, such as leaves, herbs, and newly sprouted plants (Hjeljord et al., 1990). In winter, the selection of forage available is much more restricted, and they feed mainly on twigs from deciduous trees (Cederlund, 1980; Shipley et al., 1998), as there is very little conifer forest in the study area. In Nikkaluokta, most of the open habitat is tundra, with grass, dwarf shrubs, moss and lichen. Forested areas should therefore offer higher forage availability for the moose as a browser. However, in Vistas valley (low human disturbance) moose selected open habitats more than in Ladtjo valley (high human disturbance) during the summer and winter peak tourism seasons. For *Winter Peak* period, this could indicate that snow depth is lower in the open areas, as a result of wind-induced snow transport processes (Lehning et al., 2008). This could expose the lower vegetation for forage as well as allow for easier movement.

The increased wind speed in the open areas could also reduce the insect harassment in the summer. Reindeer have been found to alter their habitat utilisation in preference of insect relief (Skarin et al., 2004). Although it has been suggested to affect moose habitat selection (Laurian et al., 2008; Morris, 2014), it has not been evident in a study. Morris (2014) found a pattern in insect intensity and moose preference of water, but as this coincided with warm temperatures it was not possible to say if insect harassment had a part in it. The insect avoidance theory would explain why moose in my study are using more open habitats in Vistas valley (low human disturbance) during the *Summer Peak* period. Future studies could look at habitat selection in response to insect levels to investigate a connection. As insect harassment can be energetically costly (Witter et al., 2012), this is something that should be considered if moose are displaced from open habitats due to disturbance by humans.

My results show *Winter Peak* season as the only period without a significant difference between the valleys. In the other periods, moose have significantly larger home ranges in Ladtjo valley than in Vistas valley. Home ranges of moose have previously been found to be consistently larger during summer than winter, partly due to an increase in home range with increasing daylight (i.e. summer) and a decrease in home range with increasing snow depth (i.e. winter) (van Beest et al., 2011). Regarding the potential tourism impact, the low seasons (*Spring Low* and *Autumn Low*) can be regarded as baselines; during these periods, the moose should not be exposed to much human activity in either of the valleys. *Summer Peak* season

shows similar differences between the valleys as the Low seasons. This is in contrast to what I hypothesised: if the moose were impacted by the tourism, I would expect them to have larger home range sizes in Ladtjo valley (high disturbance) during the peak seasons than during the low seasons, as moose have been found to increase home ranges when disturbed (e.g. Andersen et al., 1996; Harris et al., 2014). There is thus no evidence for tourism so far affecting the home range sizes of the moose.

4.1.2. Diurnal patterns of activity and rate of movement

The fact that moose were more active and had higher rates of movement at dusk than at daytime in all seasons (excluding *Spring Low* as it did not contain dusk and dawn) is explained by crepuscular activity patterns reported in moose and other ungulates (Cederlund, 1989; Neumann et al., 2012). *Summer Peak* is the only season that does not show this expected increase at dawn. This could potentially be due to dawn and dusk occurring very close together as this season is in the aftermath of the summer solstice. Other studies have found ungulates to have a weak circadian clock but are instead acutely sensitive to changes in the photoperiod; their activity peaks follow the light changes instead of anticipating them (Stokkan et al., 2007; Ensing et al., 2014; Græsli et al., 2020)

Nightly activity and rate of movement both varied between the seasons with no obvious connection to tourism intensity. The overall pattern was that moose are more active at night during summer than during winter. This in line with previous research on activity patterns in moose and other ungulates, as the warmer temperatures during the summer days make the night more favourable (Hazlerigg and Tyler, 2019; Montgomery et al., 2019). However, Ensing et al. (2014) concludes that factors such as human disturbance and weather can cause a population to be more active at night. The altering of temporal activity patterns in response to perceived predation risk has also been found both in other ungulates and in other taxa (Zapata-Ríos and Branch, 2016; Higdon et al., 2019). These patterns are not evident in my study. As the activity is measured through acceleration, this should also register if there was a difference in vigilance and alertness, even if the moose remained stationary. There is furthermore no difference in nightly activity between the contrasting valleys. This indicates that human activity is of less importance in regulating daily activity and movement patterns in the moose population than the sunlight cycle, in contrast to what I hypothesised.

4.1.3. Environmental impacts on activity and movement rates

Although the majority of the environmental factors turned out to be significant, all had low estimate values and thus negligible impacts on moose activity and speed. Several previous studies have shown that moose respond to warming temperatures by moving less to avoid overheating (e.g. Dussault et al., 2004; Ericsson et al., 2015; Montgomery et al., 2019). They also show an increase in heart rate with increasing temperatures (Græsli et al., 2020; Spong et al., 2020). I do not believe that my results challenge this view but could instead be explained by that I analysed each of the environmental factors in the form of daily averages; the ambient temperature in the study area can vary substantially between night and day, meaning that the peak temperatures do not get picked up in my analysis. In retrospect, using daily maximum temperatures instead of daily averages would potentially have given more indicative results.

The increase in temperatures is predicted to be higher in the northern alpine areas, and more so in the winter than summer (SMHI, 2019a). This will likely narrow the period when high quality forage is available for the moose (Pettorelli et al., 2007). Alpine herbivores tend to move along the elevation gradient, following the green wave of gradual onset of plant growth (Merkle et al., 2016). As forage quality is at its highest in the early phenological phases of the vegetation (Van Soest, 2018), this allows for maximisation of both quality and quantity of forage (Merkle et al., 2016; Mysterud et al., 2017). A warming climate could reduce this spatial heterogeneity in vegetation growth, which shortens the period of optimal foraging conditions. In addition, warmer temperatures increase the rate at which the plants grow, narrowing this window even further. This has been found to have a negative impacts on juvenile growth in alpine ungulate populations (Pettorelli et al., 2007).

4.2. Limitations and alternatives to my study

4.2.1. Home range extent

Although I compare two valleys with different levels of human activity, moose home ranges extended outside the valley. As a result, all analyses in my study also include these areas surrounding the valleys, even though I removed the moose individuals who used both valleys. An alternative would have been to restrict the GPS-positions to within the valleys. However, this would have given a skewed image of the moose's home range. Furthermore, I would not have been able to see whether moose favoured habitats outside the valleys during certain tourism seasons. I therefore decided to include the full home range of the moose. For future studies,

researchers can consider including a separate analysis with a subset of the data from within the two valleys to investigate differences in the results.

4.2.2. Guest nights as a way to measure tourism pressure

I used guest nights from 21 accommodation facilities in the vicinity of the study area. Guest nights are used as a proxy for tourism pressure in the valleys; this allowed me to include tourism data for the full period the moose have been monitored and allowed the study to be performed at a large spatial scale. However, it is impossible to know where each tourist went and whether they came close enough to the moose to impact moose behaviour. An alternative would be to investigate a direct connection, such as observing how the GPS-data changes when a known person approaches, as has been done in experimental studies (e.g. Neumann et al., 2011). This would either limit the temporal and spatial scale of the study as well as the sample size or require an unrealistically large effort with accompanying costs. A third option could be a type of citizen science, where hikers in the valleys voluntarily submit GPS-data from their visits. Perhaps this could be done through a hiking application on their smartphone that tracks their route from start to finish. With enough participation, and after some years with continuous moose monitoring, this could prove to be an advantageous approach.

To ensure anonymity for individual tourism facilities, I was required to select a minimum number of accommodation facilities in order to receive the data on guest nights. There are only a few accommodation facilities within and in close proximity to the study area, which resulted in a selection of facilities from a larger area than desired. Although it is still an indication of tourism pressure, it is less specific and thus risk being less accurate. In addition, some of the mountain stations nearest to the study area were closed during the period of low tourism. This would mean that during *Spring Low* and *Autumn Low* season, number of guest nights would have been zero if I had not expanded the area for accommodation facilities. This has the likely result that even fewer tourists visited the valleys during the low-seasons and should therefore not impact my results substantially.

A further consideration is that the tourism seasons that I subdivided the data into contain a varying number of days (*Winter Peak* = 88, *Spring Low* = 38, *Summer Peak* = 47, *Autumn Low* = 65). This could potentially have an effect on the comparison between the valleys. By including a longer period of the climatic seasons within a subdivided period, the factors influencing moose movement and activity could have a greater variation, as available forage and ground cover may change. However, as the primary interest was tourism pressure, the alternative to divide the periods evenly could have compromised the aim of the study, as the

subdivided periods would not accurately represent the tourism peaks and lows throughout the calendar year. In addition, as I included several environmental variables in my model, the analysis showed the importance these had on moose movement and activity, even within the subdivided periods.

4.2.3. Weather data

Regarding the weather data, I used daily averages from a weather station in the study area. Although estimates on air temperature were registered by the GPS-collars on the moose, the remaining weather variables were solely taken from the weather station. It is therefore possible that the precipitation and wind speed recorded at the weather station differed from the precipitation and wind speed experiences by a moose at a given place and time. However, the weather station's data gives a good indication of the weather conditions in the area as it is unlikely to differ with extreme amounts. The air temperature recorded from the GPS-collar has previously been shown to have a known off-set from the actual air temperature, although following the same curve (Ericsson et al., 2015), and have been used in other studies (e.g. Montgomery et al., 2019). Future studies should focus on maximum temperatures rather than averages, in line with Montgomery et al. (2019). This is something to consider for other weather variables as well.

4.2.4. The acceleration data

Measuring acceleration data from sensors as a means to extrapolate behaviours is a fairly novel method that is still under development. It has the benefits over direct observations (e.g. Van Ballenberghe and Miquelle, 1990) and radio-telemetry signals (e.g. Cederlund, 1989) in that the measured activity does not risk being affected by the presence of the observer, and it makes it possible to collect continuous long-term data (Krop-Benesch et al., 2013). However, there are large variations in how studies transform and analyse the raw acceleration data collected from GPS-sensors (e.g. Fehlmann et al., 2017; Yang et al., 2018; Benoit et al., 2020). I chose to take an average of the x and y values, in line with Berger and Dettki (2009), for a couple of reasons. First, I did not have a z-value as many of the other studies had in their more complicated formulas. Second, as I was interested in the differences between the values, the absolute values themselves did not need to be transformed into a specific unit as long as my calculations ensured the resulting values were standardised so they could be compared.

Some studies have determined what range of acceleration corresponds to a certain behaviour. This has been done for other ungulates (e.g. Heurich et al., 2012; González et al., 2015), but not for moose. If future studies determine what

acceleration value in moose that corresponds to increased vigilance, it would be possible to reanalyse my data to investigate the connection further.

An additional factor to consider when looking at movement rates and activity levels in an alpine population is the potential impact of increasing elevation on speed and acceleration. As mentioned in section 4.1.3, the moose likely follow the new growth of vegetation, resulting in a seasonal migration towards higher altitudes in spring. Furthermore, other alpine ungulate species have been found to move to higher altitudes in an attempt to escape parasitic flies and to reach cooler temperatures (e.g. Skarin et al., 2010). Even though my data did not include the altitude of the moose, it could thus be possible to infer an approximate altitude based on season, maximum temperatures, and vegetation type. This would however be an imprecise approach; a better option would be to acquire altitudinal data for each GPS-position of the moose and include it in the analysis.

An alternative way of identifying increased stress-levels of the moose in the peak tourism seasons could be to use bodily implants or samples for measuring stress hormones or physiological data (e.g., heart rate and body temperature to estimate metabolic rate and stress). Græsli et al. (2020) used subcutaneous heart rate loggers that recorded both heart rate and body temperature. Although this method limits the study to the female part of the population, it would give an insight into physiological responses to stress when it is not visible in the behaviour. Many studies have also analysed faecal samples in other ungulate species (Millspaugh et al., 2001; Zbyryt et al., 2018). Spong et al. (2020) measured stress-levels in Swedish moose populations through hair samples taken during moose hunts. As the population in Nikkaluokta also is a hunted population, either faecal collection or hair samples could be possible. It would however restrict the sampling period to that of the hunt.

4.2.5. The sunlight phases

I summarised 14 specific sunlight phases into four categories appropriate for the purpose of my study. As one of my subset periods, *Spring Low*, coincided with the summer solstice, I instead assigned night and day based on time of day. This was done with tourism pressure in mind, assuming that the majority of tourists are most active between 08.00 and 20.00. Provided this is true, it gives an adequate base for comparing day and night with the other periods. However, it does exclude the possibility of comparing dawn and dusk moose activity and movement speed with this period.

4.3. Conclusion

Considering we are in the middle of a climate crisis, even a small reduction in fitness can have detrimental consequences to a population. Many studies have shown that moose are disturbed by human recreational activities, but the long-term effect on their fitness is hard to measure. This is of growing importance, as nature-based activities are becoming increasingly popular. My study has the advantage of 12 years of moose activity and movement rate data covering the entire annual cycle, collected in two valleys contrasting in human activity, with the main limitations being the indirect measure of human disturbance. My study found a displacement of moose during the peak tourism seasons in highly frequented areas into habitats offering more protection, but I did not find any other indications that the moose were disturbed. It is possible that removing themselves from more open areas is enough; once they are in protective cover, there may not be any need for increased vigilance, movement rates, or change in diurnal activity patterns. However, it could still be detrimental to the fitness of the animals to be displaced into less favourable habitats. More physiological studies are needed to determine whether movement into protective habitats is enough to counteract other negative impacts of human disturbance, and whether this is less damaging than a physiological stress response. My findings, in combination with future research, can help managers make educated decisions on further recreational sprawl into moose habitat, such as placing of hiking trails and directing certain activities to less sensitive areas, or ensuring there are protective habitats available with good-quality forage opportunities. Furthermore, if we can predict how moose habitat selection changes when they are exposed to disturbance, smart planning of recreational activities can help reduce browsing damage to sensitive forest areas.

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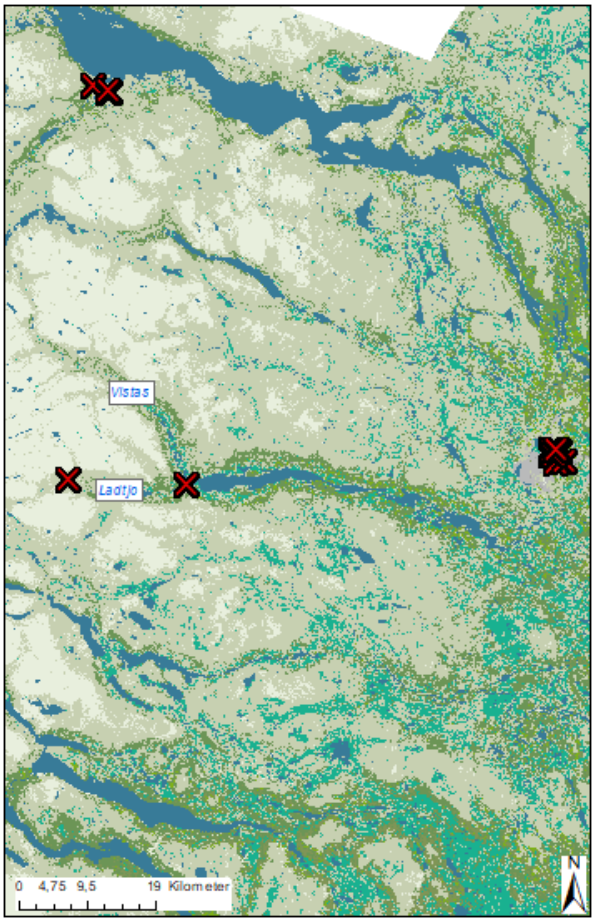
Appendix 1 – Accommodation facilities

Accommodation facilities
Abisko turiststation
Abisko Mountain Lodge
Abisko Fjällturer
Abisko Guesthouse
Nikkaluokta Sarri AB
Hotell Kebne
Scandic Ferrum
Ripan Hotell
Kebnekaise Fjällstation
Järnvägshotellet
Hotell Vinterpalatset
Samegården
Gullriset Lägenhetshotell
Hotell E:10 i Kiruna AB
Yellow House Hotell & Vandrarhem
Kirunarum och Vandrarhem
Spis Hotel & Hostel
Best Western Hotel Arctic Eden
Camp Ripan AB
Malmfälten Logi & Konferens
Kiruna Vandrarhem
Hotel Bishops Arms
STF Vandrarhem & Hotell Kiruna



Appendix 2 – Vegetation reclassifications

Original classification	Reclassification used in study
Open wetland	Open
Other open land without vegetation	Open
Other open land with vegetation	Open
Exploited land building	Other
Exploited land, not building or road/railroad	Other
Exploited land, road/railroad	Other
Lake and water ways	Water
Pine forest (outside wetland)	Conifer forest
Spruce forest (outside wetland)	Conifer forest
Mixed conifer forest (outside wetland)	Conifer forest
Mixed deciduous and conifer forest (outside wetland)	Mixed forest
Trivial deciduous forest (outside wetland)	Deciduous forest
Pine forest (on wetland)	Conifer forest
Spruce forest (on wetland)	Conifer forest
Mixed deciduous and conifer forest (on wetland)	Mixed forest
Trivial deciduous forest (on wetland)	Deciduous forest

Appendix 3 – Suncalc definitions

Original variable	Categorised as used in study
sunrise	Dawn
sunriseEnd	Dawn
golderHourEnd	Day
solarNoon	Day
goldenHour	Day
sunsetStart	Dusk
sunset	Dusk
dusk	Dusk
nauticalDusk	Dusk
night	Night
nadir	Night
nightEnd	Night
nauticalDawn	Dawn
dawn	Dawn

Appendix 4 – Influential factors

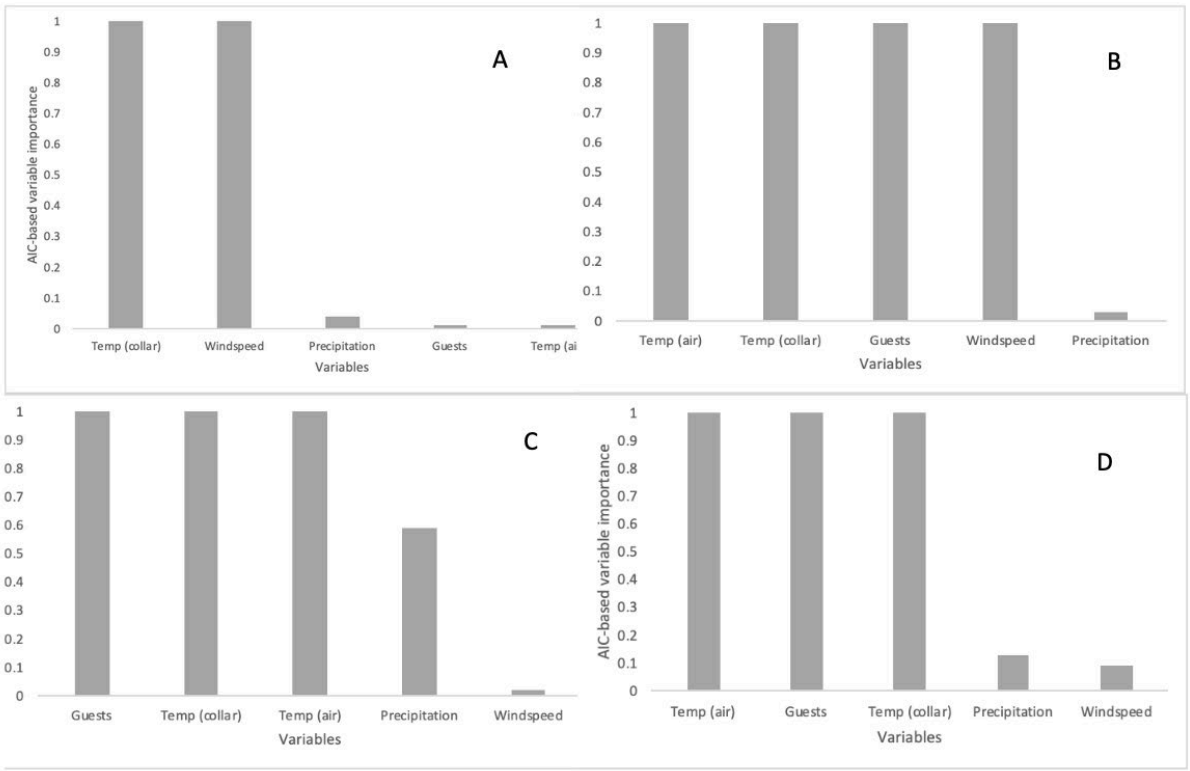


*Figure 8. The five factors most influential on **activity** (measured in acceleration) in the model determined by model averaging based on Akaike Information Criterion (AICc). A= Winter Peak, B = Spring Low, C = Summer Peak, D = Autumn Low*

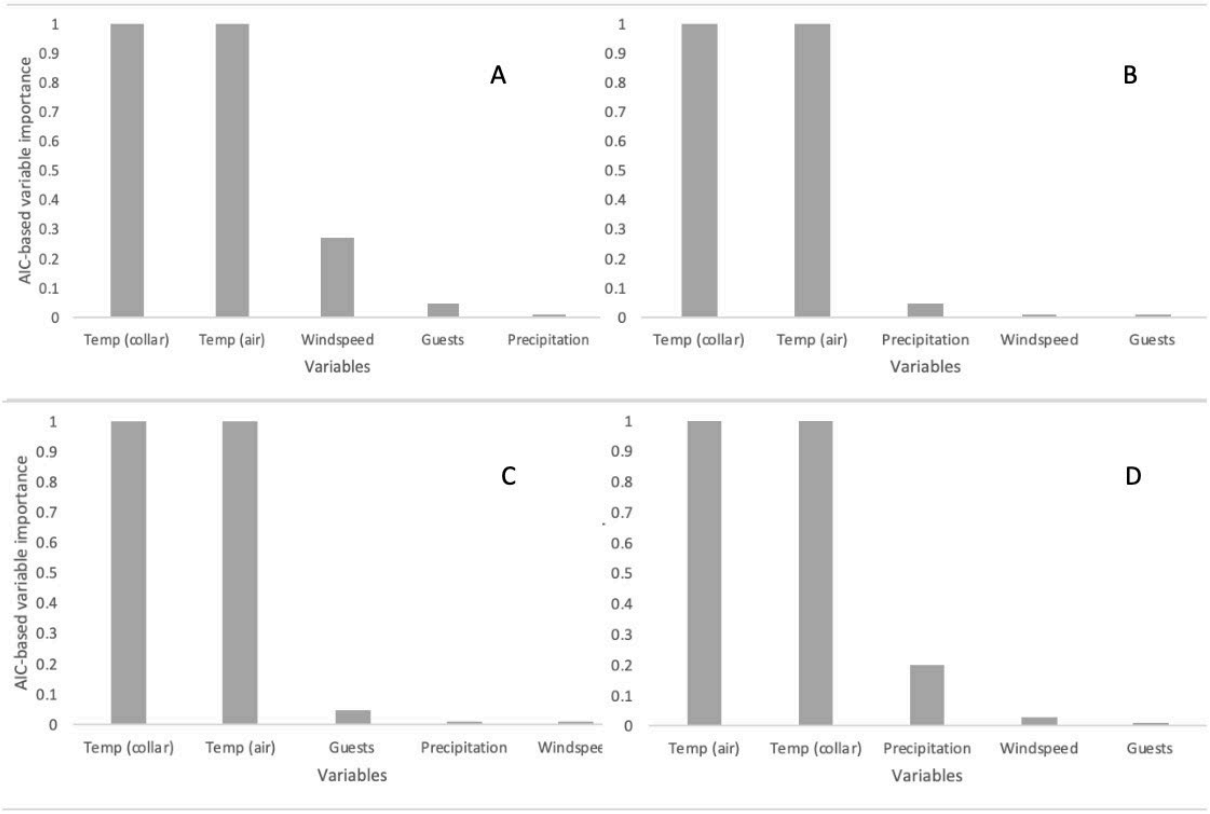


*Figure 11. The five factors most influential on **movement rates** in the model determined by model averaging based on Akaike Information Criterion (AICc) A= Winter Peak, B = Spring Low, C = Summer Peak, D = Autumn Low*

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